The role of behaviour in predator – prey interactions

Daniel Fortin, Maxime Fraser Franco, Pierre-Olivier Montiglio

Sentinelle Nord summer school

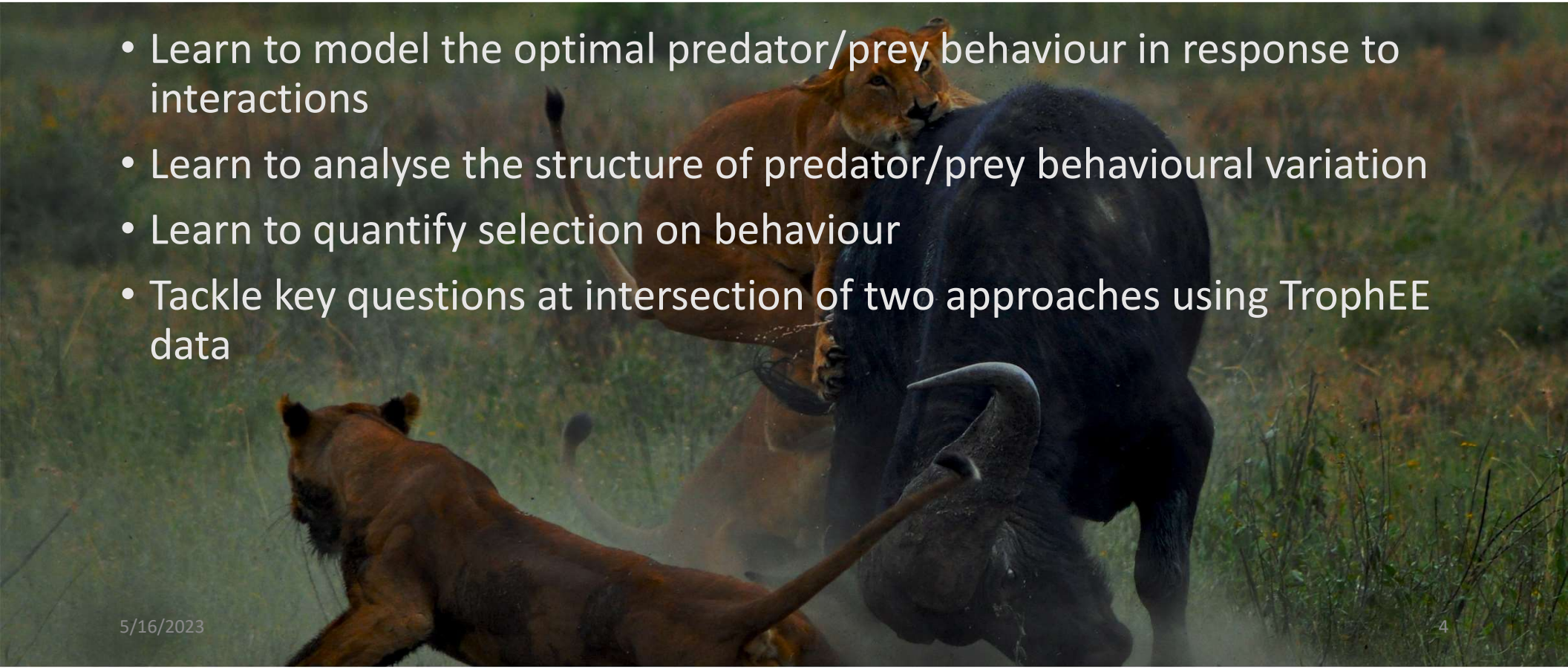
Who we are

- Daniel Fortin (Professor at Laval University)
  - Behavioural mechanisms driving animal distribution in landscape
  - Daniel's page
- Maxime Fraser Franco (PhD candidate at UQAM)
  - Drivers and consequences of individual variation in predator-prey interactions
  - Maxime's page
- Pierre-Olivier Montiglio (Professor at UQAM)
  - Evolutionary biology of interacting phenotypes
  - PO's page

Who are you?

- What is your name?
- Where do you come from?
- What are you working on?
- What are you looking for in this summer school?

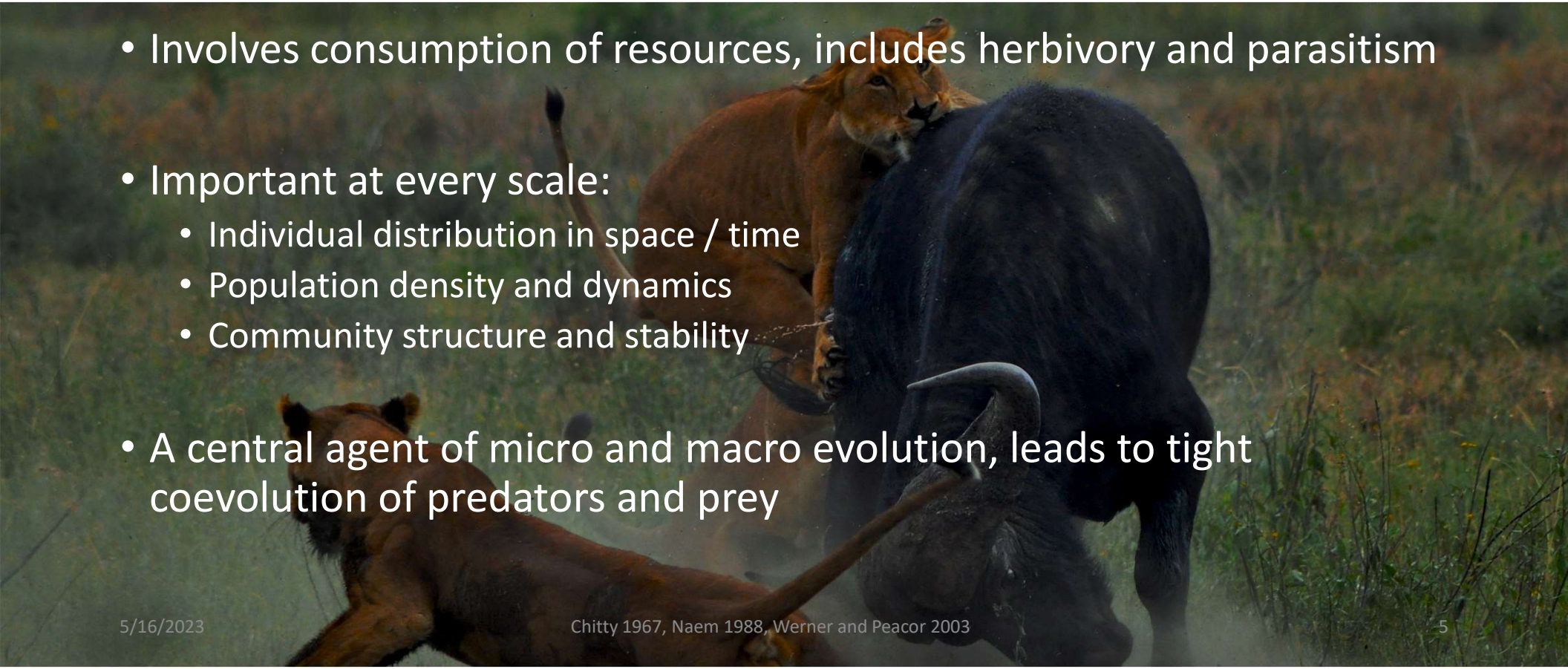
Objectives of this work package



- Learn to model the optimal predator/prey behaviour in response to interactions
- Learn to analyse the structure of predator/prey behavioural variation
- Learn to quantify selection on behaviour
- Tackle key questions at intersection of two approaches using TrophEE data

THE interaction among organisms

FM0



- Involves consumption of resources, includes herbivory and parasitism
- Important at every scale:
  - Individual distribution in space / time
  - Population density and dynamics
  - Community structure and stability
- A central agent of micro and macro evolution, leads to tight coevolution of predators and prey

Chitty 1967, Naem 1988, Werner and Peacor 2003

Diapositive 5

FM0 Consumer-resource interactions maybe?

Fraser Franco, Maxime; 2023-04-25T13:50:26.270

The evolution of predator – prey interactions

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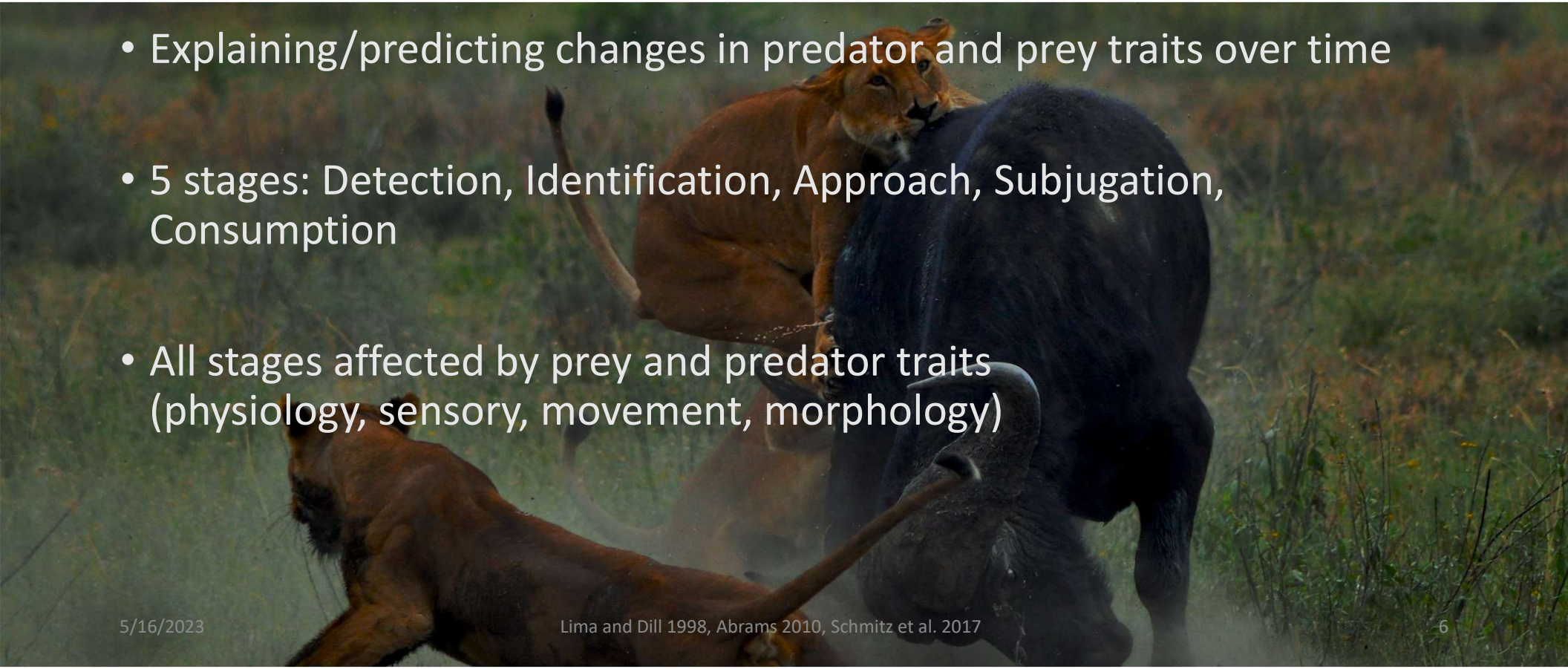


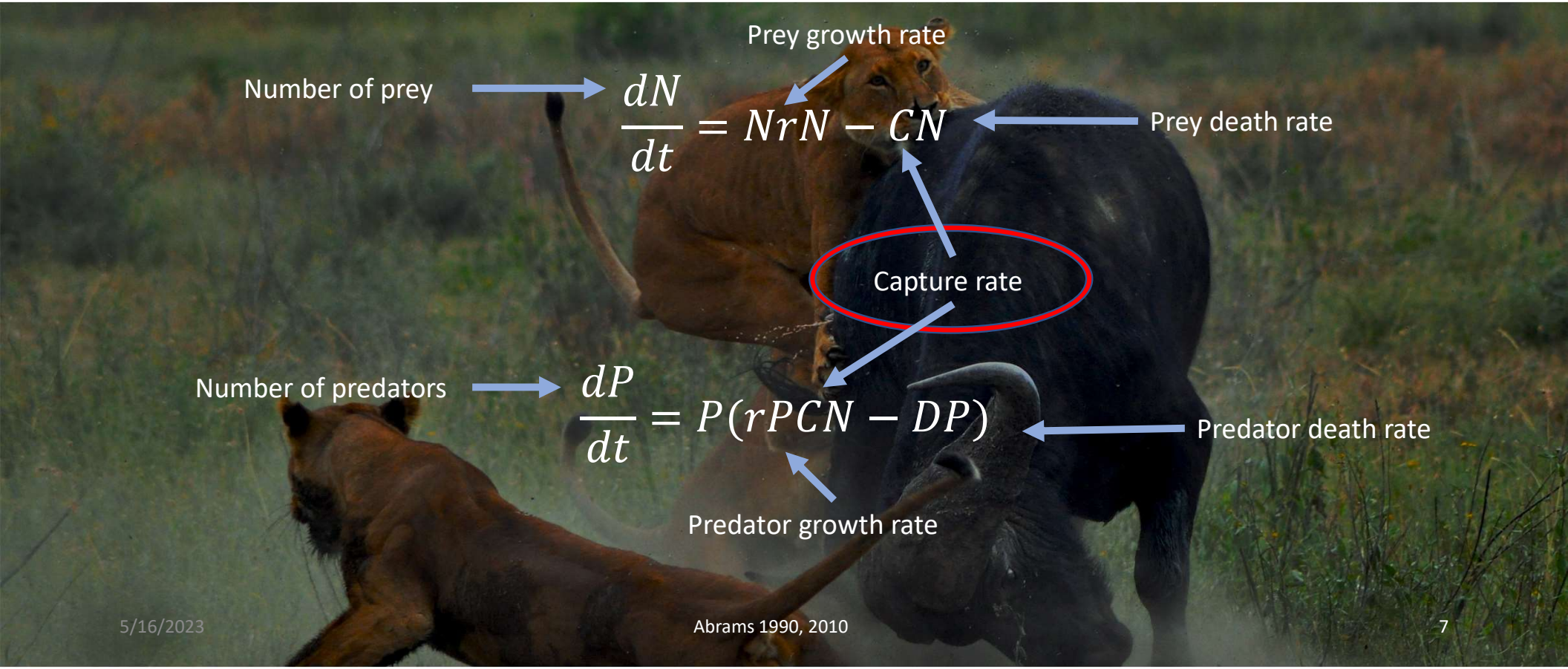
- Explaining/predicting changes in predator and prey traits over time
- 5 stages: Detection, Identification, Approach, Subjugation, Consumption
- All stages affected by prey and predator traits (physiology, sensory, movement, morphology)

Lima and Dill 1998, Abrams 2010, Schmitz et al. 2017

Diapositive 6

FM0 dynamics? juste une suggestion.
Fraser Franco, Maxime; 2023-04-25T13:51:00.457

A first model for predator – prey interactions



Prey growth rate

Number of prey

$$\frac{dN}{dt} = NrN - CN$$

Prey death rate

Capture rate

Number of predators

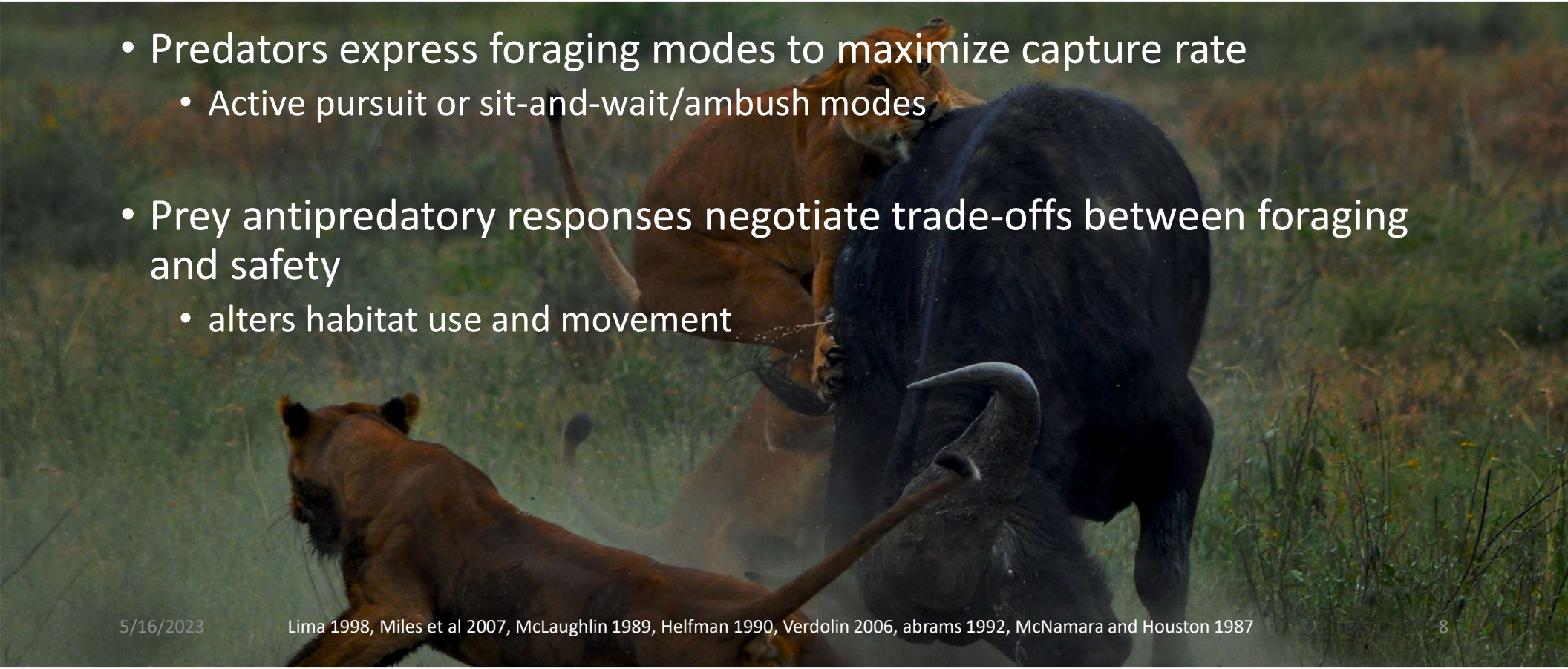
$$\frac{dP}{dt} = P(rPCN - DP)$$

Predator death rate

Predator growth rate

Abrams 1990, 2010

Studying the role of behaviour in predator – prey interactions



- Predators express foraging modes to maximize capture rate
  - Active pursuit or sit-and-wait/ambush modes
- Prey antipredatory responses negotiate trade-offs between foraging and safety
  - alters habitat use and movement

Lima 1998, Miles et al 2007, McLaughlin 1989, Helfman 1990, Verdolin 2006, abrams 1992, McNamara and Houston 1987

Two approaches to analyse behaviour

FM0

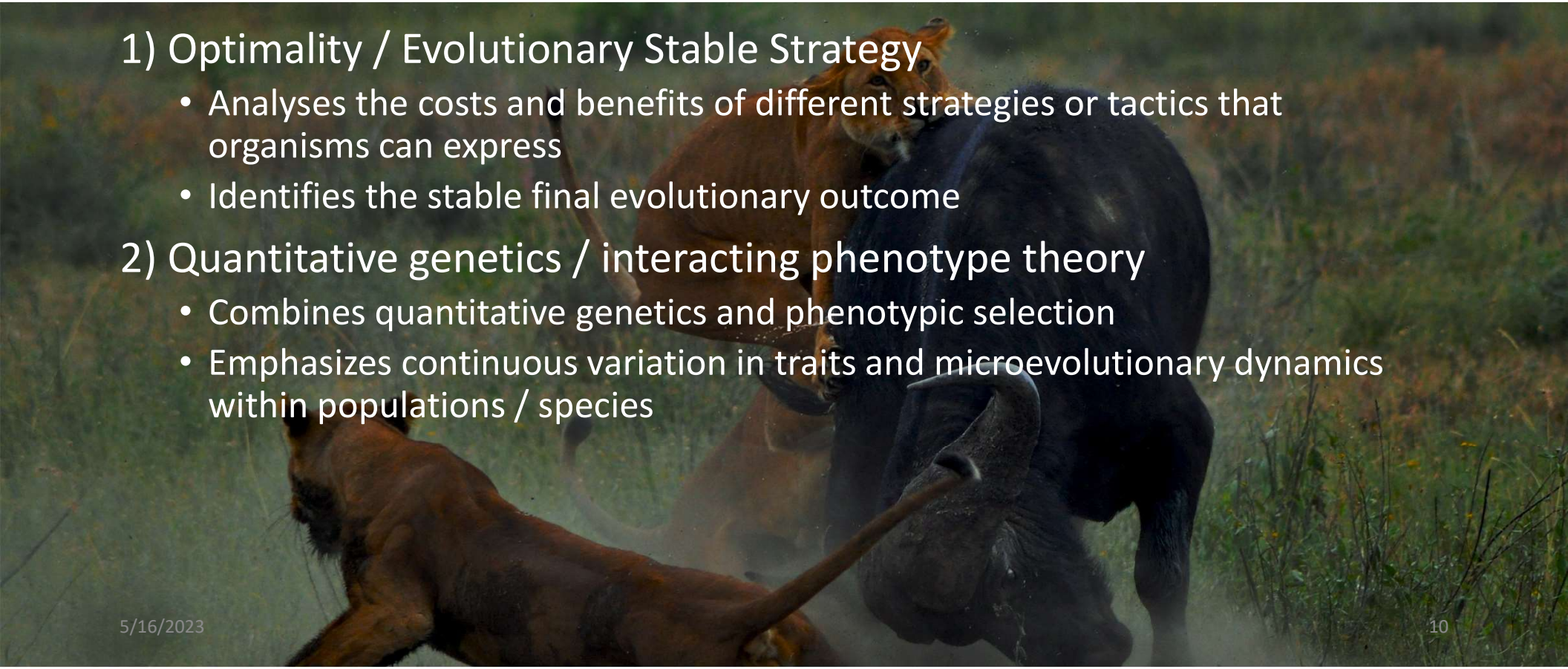
1) Optimality / Evolutionary Stable Strategy
   - Analyses the costs and benefits of different strategies or tactics that organisms can express
   - Identifies the stable final evolutionary outcome

Diapositive 9

FM0 Two approaches in behavioural ecology maybe? Car les autres "work package" vont aussi analyser le comportement d'une certaine façon.

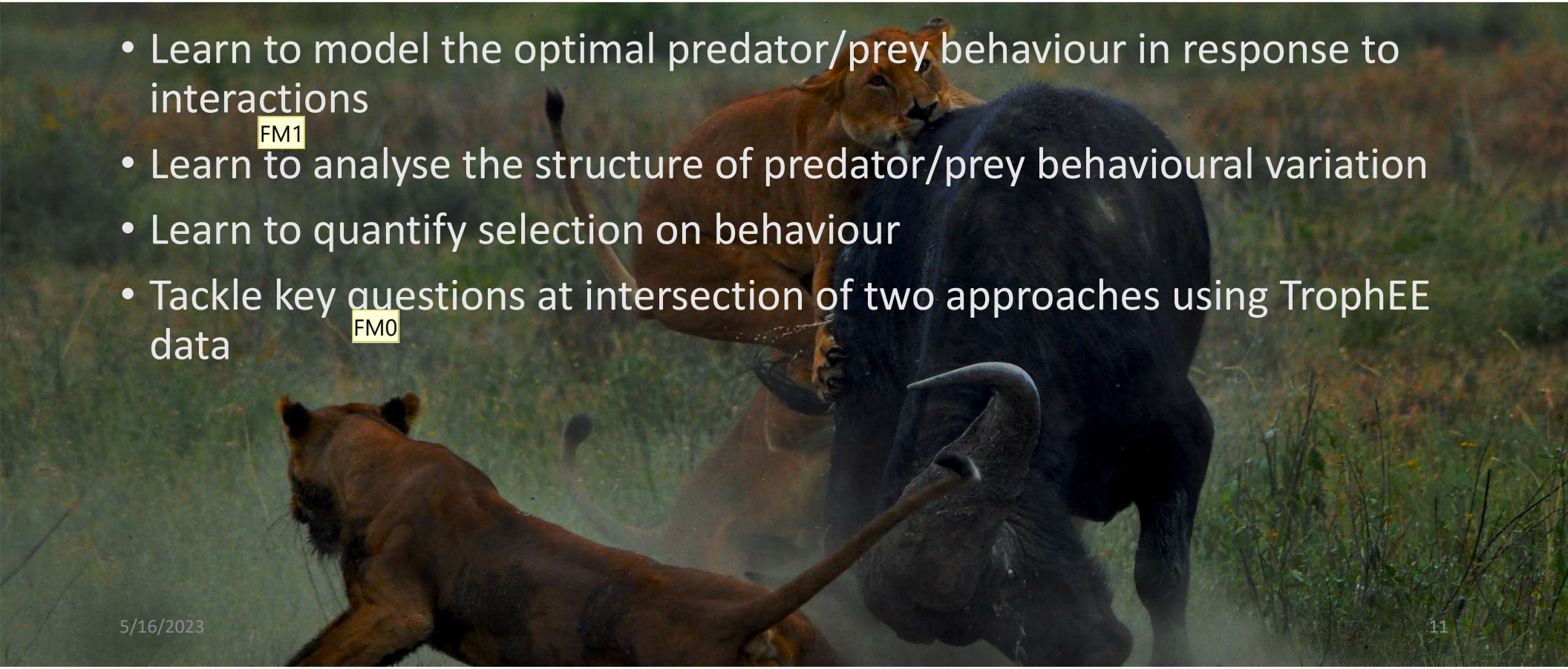
Fraser Franco, Maxime; 2023-04-25T13:52:45.519

Two approaches to analyse behaviour



1) Optimality / Evolutionary Stable Strategy
   - Analyses the costs and benefits of different strategies or tactics that organisms can express
   - Identifies the stable final evolutionary outcome
2) Quantitative genetics / interacting phenotype theory
   - Combines quantitative genetics and phenotypic selection
   - Emphasizes continuous variation in traits and microevolutionary dynamics within populations / species

Objectives of this work package



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Diapositive 11

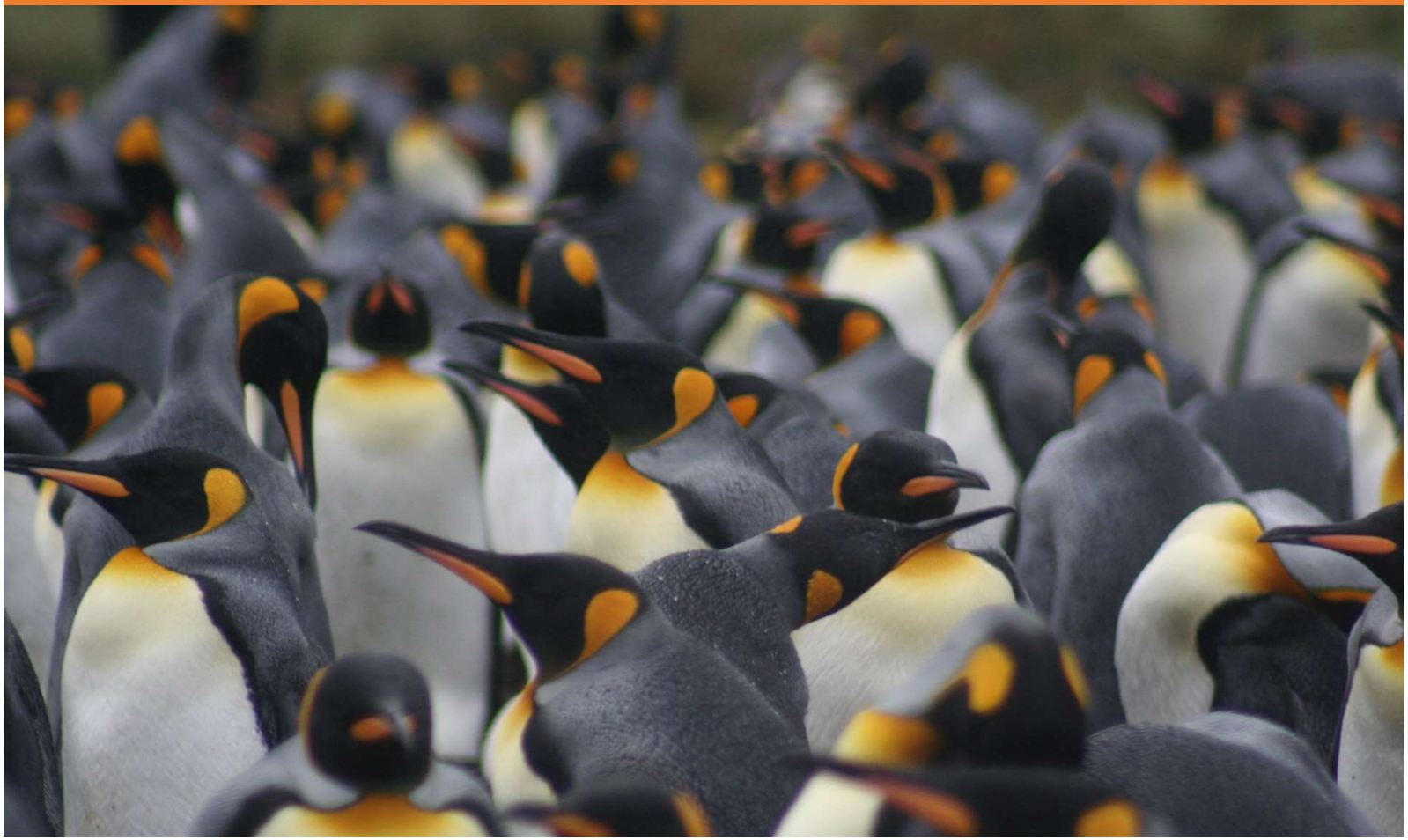
FM0 Je trouve que cette phrase n'est pas très claire.
Fraser Franco, Maxime; 2023-04-25T13:53:40.784

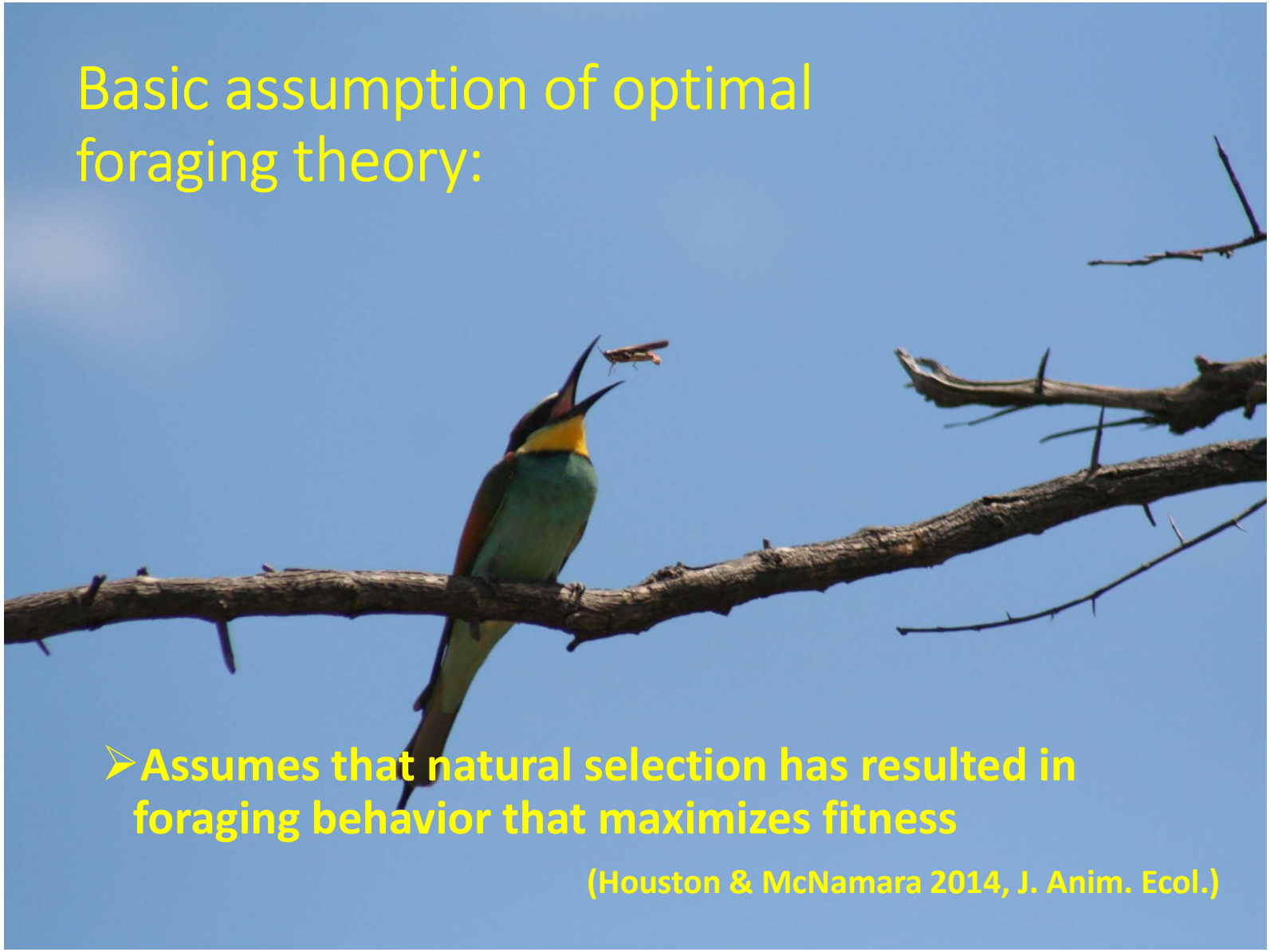
MPO0 0 Mieux comme ça?
Montiglio, Pierre-Olivier; 2023-04-26T18:29:45.192

FM1 Il y a beaucoup de "bullet points" et d'autres imbriqués dans des "bullet points" à travers les slides qui rendent la lecture difficile. Ici par exemple, on en combine deux (point + chiffre). Peut-être épurer un peu pour aider la lecture
Fraser Franco, Maxime; 2023-04-25T14:02:03.453

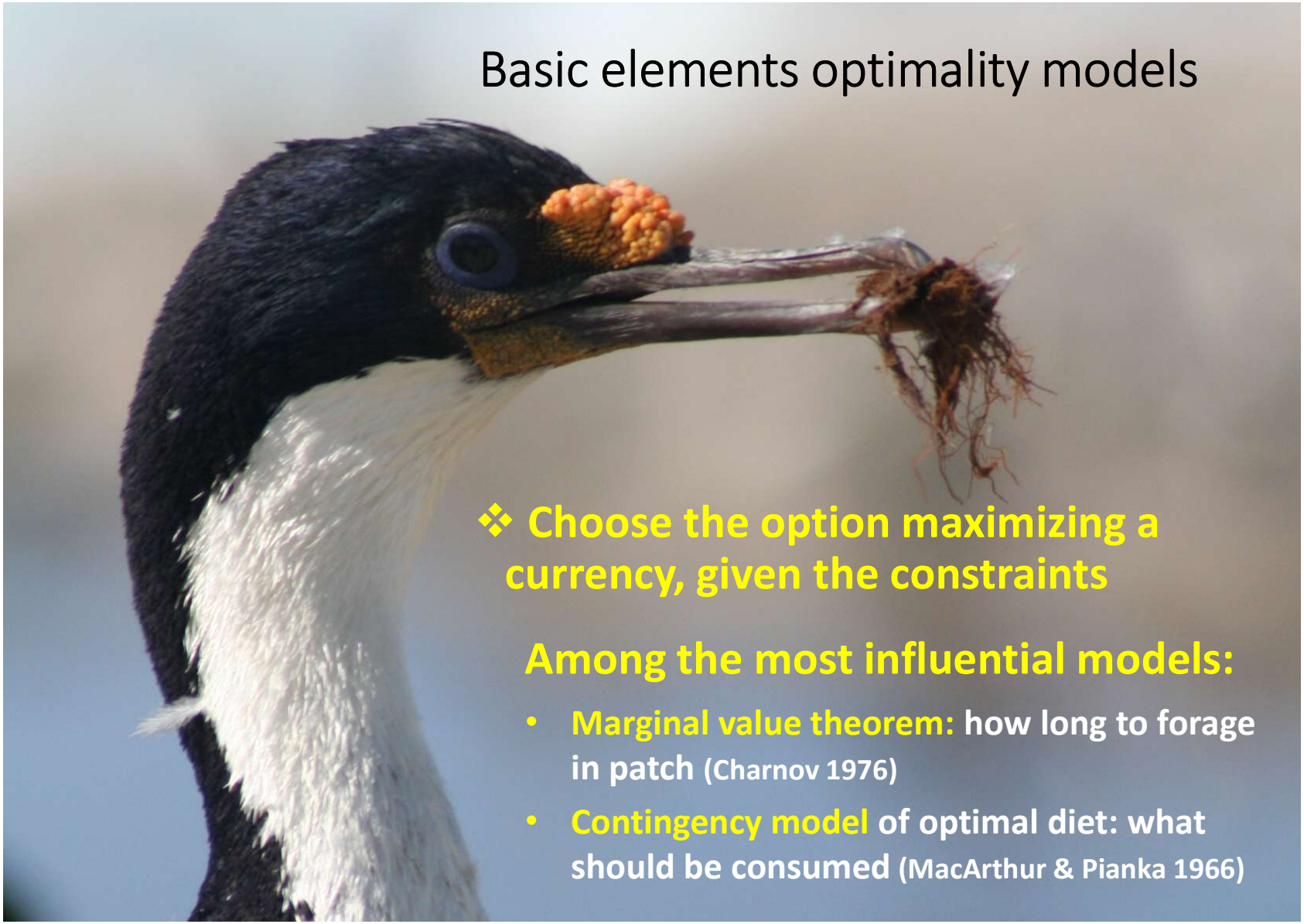
MPO1 0 Mieux comme ceci? On a 4 points généraux maintenant
Montiglio, Pierre-Olivier; 2023-04-26T18:30:01.422

1) Optimal foraging under predation risk




Basic assumption of optimal foraging theory:
➢Assumes that natural selection has resulted in foraging behavior that maximizes fitness
(Houston & McNamara 2014, J. Anim. Ecol.)

Basic elements optimality models



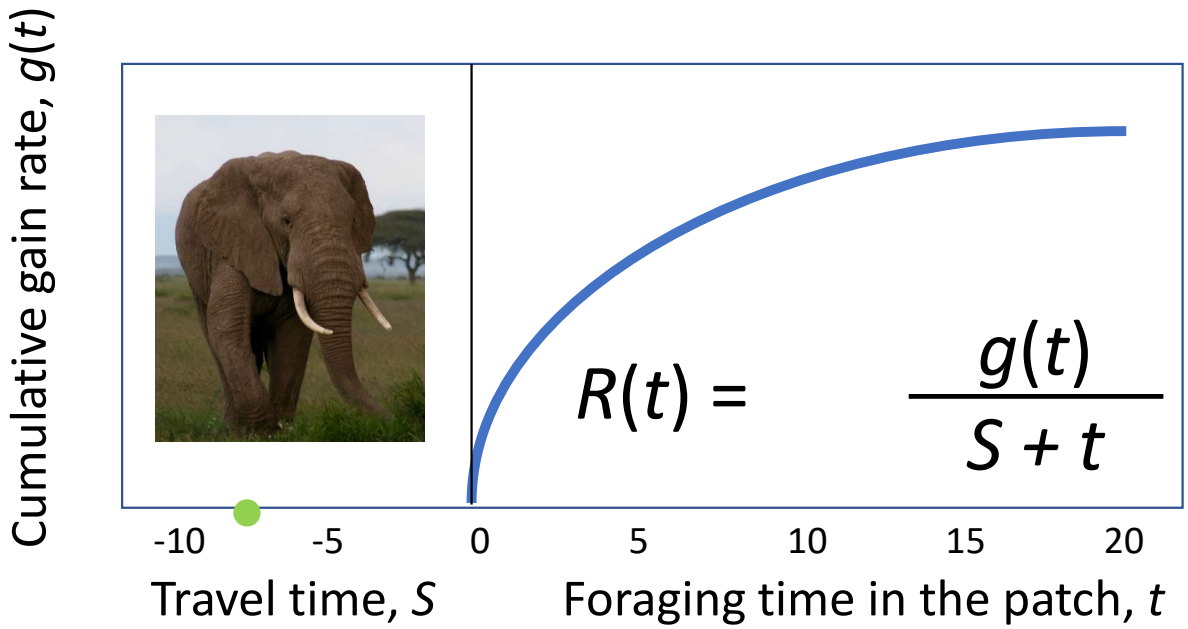
❖ **Choose the option maximizing a currency, given the constraints**

Among the most influential models:

- **Marginal value theorem: how long to forage in patch (Charnov 1976)**
- **Contingency model of optimal diet: what should be consumed (MacArthur & Pianka 1966)**

Optimal patch departure time
Marginal value theorem

Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. Theoretical Population Biology 9:129-136.



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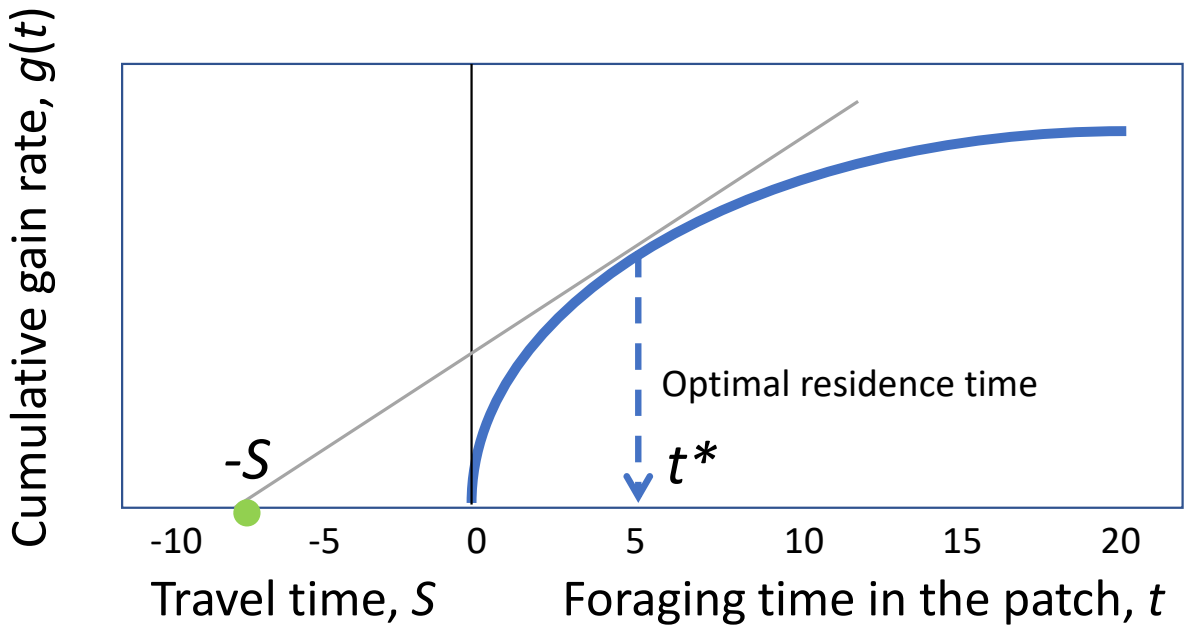
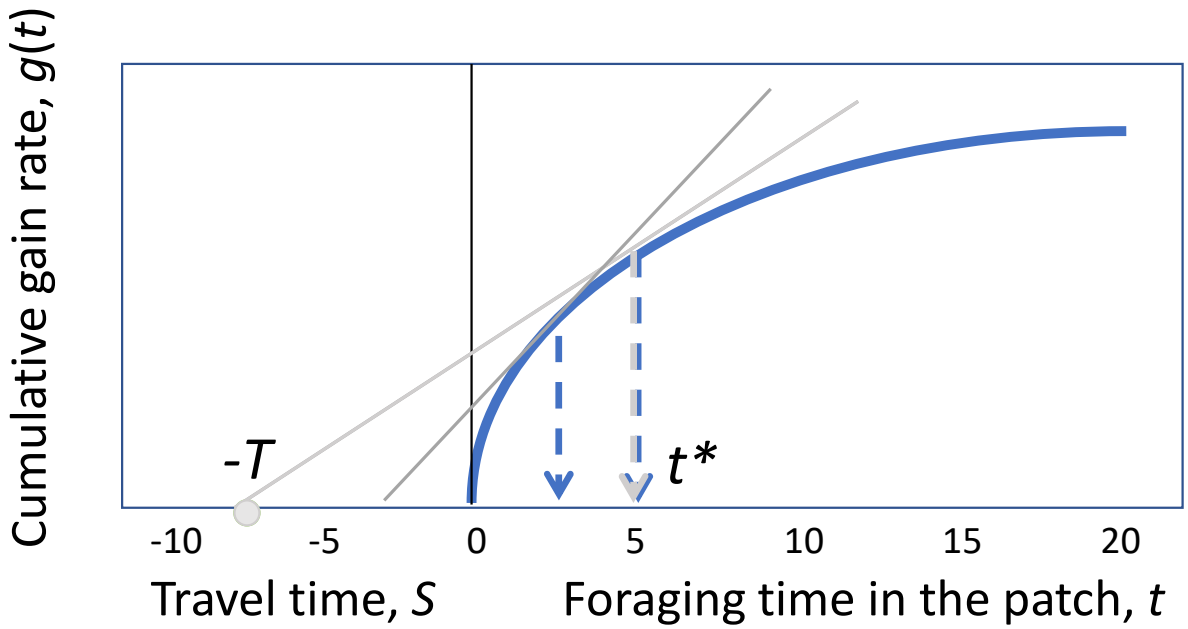


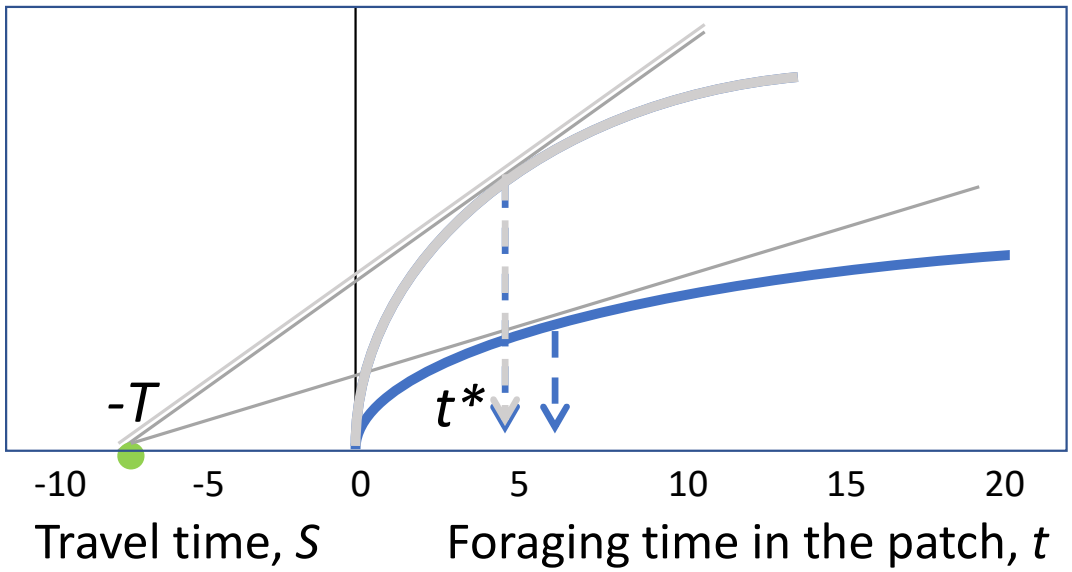
Optimal patch departure time
Marginal value theorem

Lower average time to move between patches



Optimal patch departure time
Marginal value theorem

Lower performance of the consumer



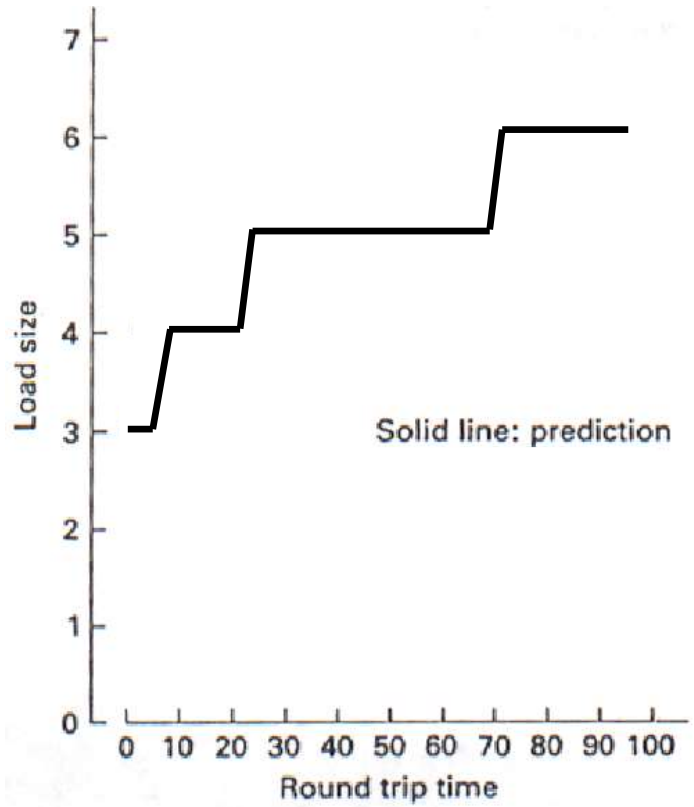
Optimal patch departure time
Marginal value theorem

Variation in mealworm load size, given the distance from the nest

Kacelnik (1984, Journal of Animal Ecology 53: 283-299)

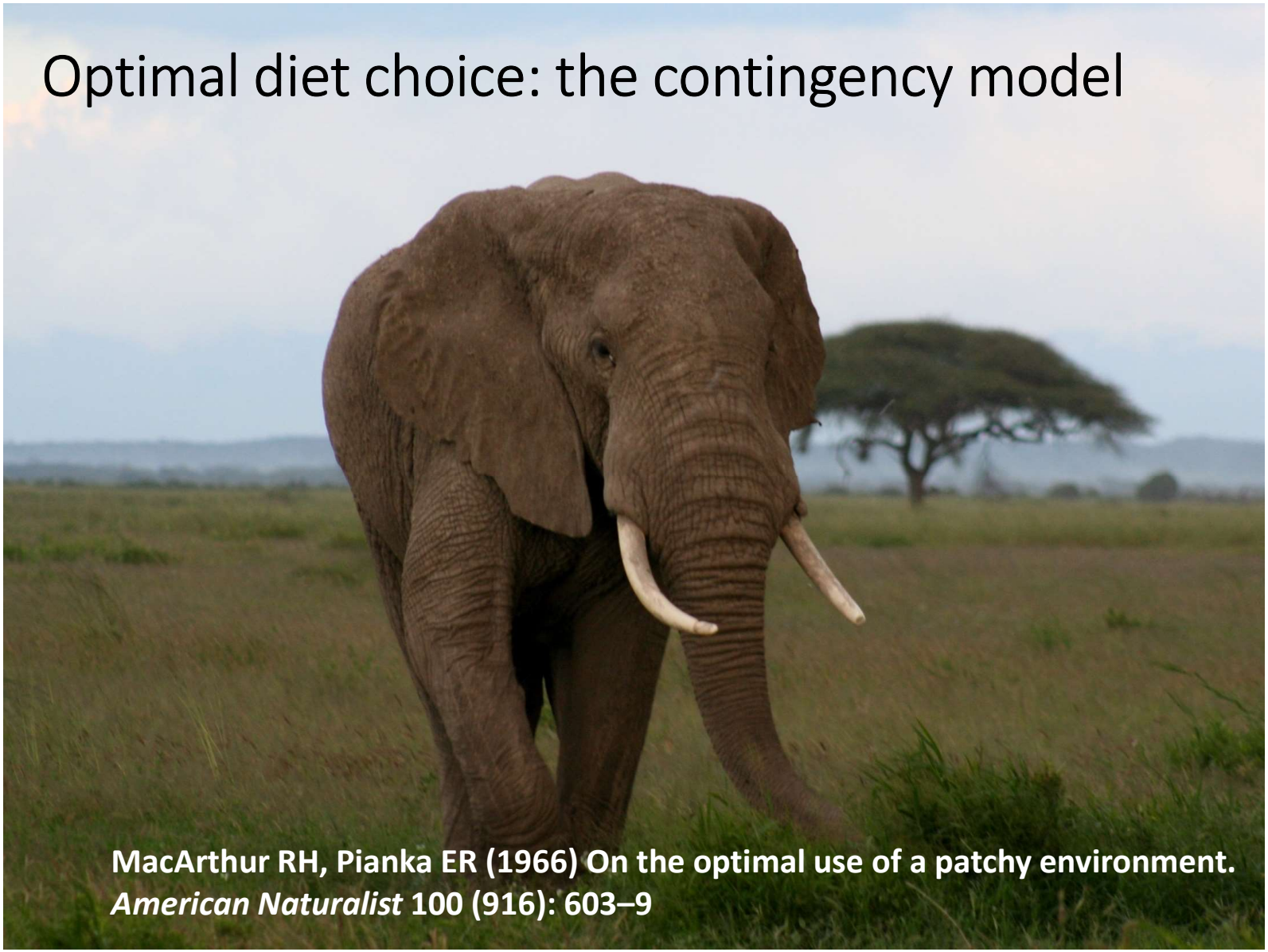
Optimal patch departure time
Marginal value theorem

- Place feeding trays with mealworms at different distances from the nest
- Induce a decrease in worm capture rate with time spent in the patch; he manipulated the gain function
- **How should load size vary with the distance from the nest**
  - **Model predicts larger loads with longer travel times**



Kacelnik (1984, J. Anim. Ecol. 53: 283-299)

Optimal diet choice: the contingency model



MacArthur RH, Pianka ER (1966) On the optimal use of a patchy environment. *American Naturalist* 100 (916): 603–9

Estimation of the rate of energy intake

$$E = e\frac{F}{T_f} = e\boxed{I}$$

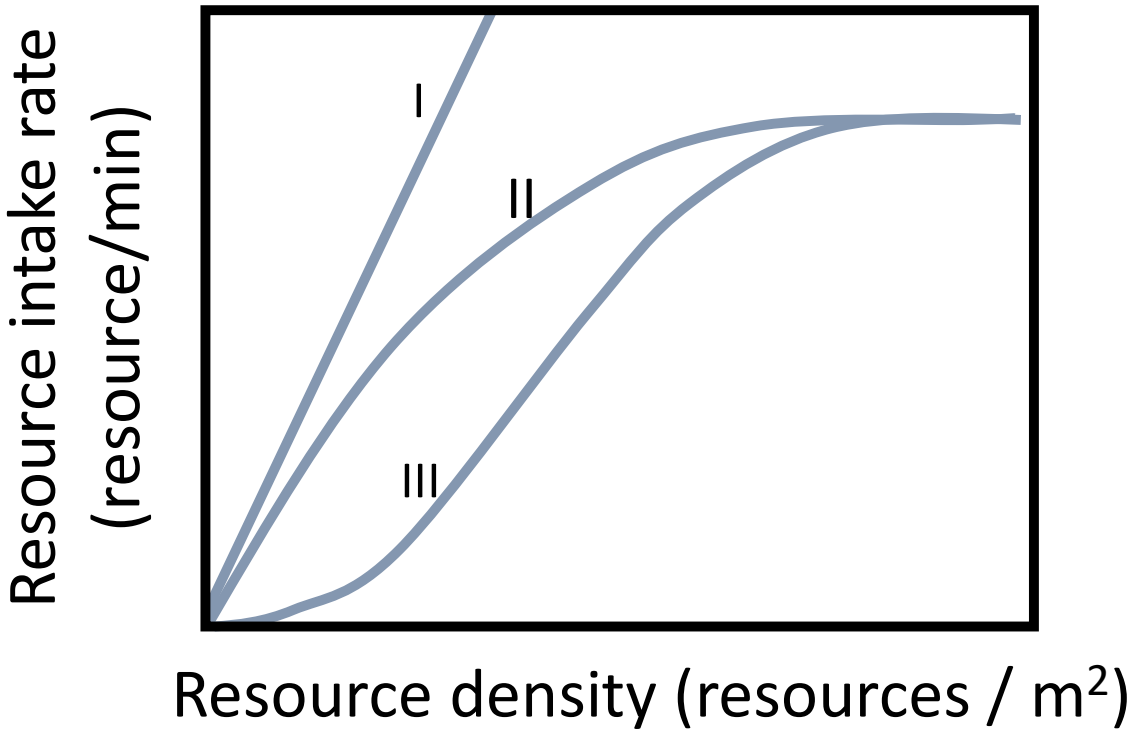
E: Energy intake rate (kJ / min), *F*: Number of prey consumed (prey), T_f: Total foraging time (min), *e:* Energy content (kJ / prey)

$F / T_f = I$ = Prey intake rate (prey / min)

Energy intake rate = (Intake rate of a given prey type) **X** (energy content)

Related to functional responses

Main types of functional response



Mechanistic functional response

$$I = \frac{F}{T_f} \qquad I = \frac{aNT_s}{T_s + T_h}$$

- $T_f = T_s + T_h$
- a: Search rate, e.g., area over which prey can detect per unit of time (m^2/min)
  - Speed (m /min) x detection radius (m)
- N: Resource density (resources / m^2)
- T_s: Total time spent searching (min) during T_f
- T_h: Total time species handling (min) during T_f

Mechanistic functional response

$$I = \frac{F}{T_f} \qquad I = \frac{aNT_s}{T_s + \boxed{aNT_s \times h}}$$

- $T_f = T_s + T_h$
- a: Search rate, e.g., area over which prey can detect per unit of time (m^2/min)
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- N: prey density (prey/ m^2)
  - T_s: Total time spent searching (min) during T_f
  - T_h: Total time species handling (min) during T_f
    - $T_h = aNT_s \times h$,

      where h: time needed to handle each prey (min / prey)

Multispecies mechanistic functional response

$$I = \frac{aNT_s}{T_s + aNT_s \times h} \qquad I = \frac{aNT_s}{T_s + aNT_s \times h}$$

$$I = \frac{aT_s \sum_{i=1}^{M} (N_i p_i)}{T_s + aT_s \sum_{i=1}^{M} (N_i h_i p_i)} = \frac{a \sum_{i=1}^{M} (N_i p_i)}{1 + a \sum_{i=1}^{M} (N_i h_i p_i)}$$

Where p_i indicates whether (value of 1) are not (value of 0) type i prey is consumed whenever encountered

What if multiple prey types can be consumed?

Maximization of energy intake rate: the contingency model

$$I = \frac{aT_s \sum_{i=1}^{M} (N_i p_i)}{T_s + aT_s \sum_{i=1}^{M} (N_i h_i p_i)} = \frac{a \sum_{i=1}^{M} (N_i p_i)}{1 + a \sum_{i=1}^{M} (N_i h_i p_i)}$$

We can estimate *E* for a diet of *M* resource types by multiplying *e* of each resource type following:

$$E = \frac{a \sum_{i=1}^{M} (N_i p_i e_i)}{1 + a \sum_{i=1}^{M} (N_i h_i p_i)}$$

Maximization of energy intake rate: the contingency model

$$E_{total} = \frac{a\sum_{i=1}^{M}(N_i p_i e_i)}{1 + a\sum_{i=1}^{M}(N_i h_i p_i)}$$

Let's evaluate a diet comprised of two resource types:

$$\boxed{E_{total} = \frac{a(N_1 p_1 e_1 + N_2 p_2 e_2)}{1 + a(N_1 h_1 p_1 + N_2 h_2 p_2)}}$$

We can assume that the profitability of type 1 resource is higher than that for type 2 resource, i.e., $e_1/h_1 > e_2/h_2$. Which diet would then yield the maximum energy gain?

Maximization of energy intake rate: the contingency model

$$E = \frac{a(N_1 p_1 e_1 + N_2 p_2 e_2)}{1 + a(N_1 h_1 p_1 + N_2 h_2 p_2)}$$

Let's now evaluate how energy intake rate varies with the consumption of type 1 resource:

$$\frac{\partial E}{\partial p_1} = \frac{(e_1 h_2 - e_2 h_1) p_2 a^2 N_1 N_2}{(1 + p_1 a h_1 N_1 + p_2 a h_2 N_2)^2}$$

Because $e_1/h_1 > e_2/h_2$, $\frac{\partial E}{\partial p_1}$ can only be positive…

… type 1 resource should therefore always be consumed to maximize E

Maximization of energy intake rate: the contingency model

$$E = \frac{a(N_1 p_1 e_1 + N_2 p_2 e_2)}{1 + a(N_1 h_1 p_1 + N_2 h_2 p_2)}$$

We can evaluate how energy intake rate varies with the consumption of type 2 resource :

$$\frac{\partial E}{\partial p_2} = \frac{a N_2 (e_2 + p_1 e_2 a h_1 N_1 - p_1 e_1 a h_2 N_1)}{(1 + p_1 a h_1 N_1 + p_2 a h_2 N_2)^2}$$

Consuming type 2 resource increase energy gains (i.e., $\frac{\partial E}{\partial p_2} > 0$) when…

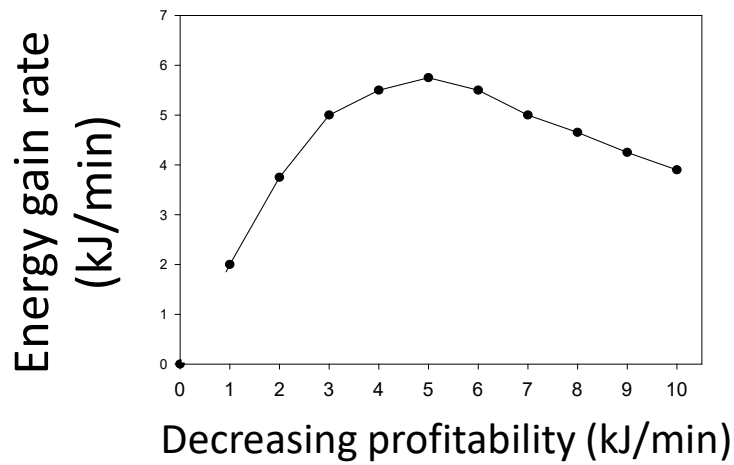
λ_1

Encounter rate

$$N_1 a < \frac{e_2}{e_1 h_2 - e_2 h_1}$$

Type 2 resource should not be consumed if the abundance of type 1 resource is relatively high

Maximization of energy intake rate: the contingenty model



Change in energy gain rate following the successive addition of resource types in the diet, in order of decreasing profitability

$$E = \frac{a\sum_{i=1}^{5}(N_i e_i)}{1 + a\sum_{i=1}^{5}(N_i h_i)} > \frac{e_6}{h_6} > \cdots > \frac{e_{10}}{h_{10}}$$

Maximization of energy intake rate: the contingenty model

- Optimal choice depends on the encounter rate with the optimal resource types
  - Change in the availability of the less profitable types does not influence the optimal diet
  - Associated with the principle of missed opportunity costs
- A given resource type should always be consumed or ignored encountered, i.e., 0-1 rule

Maximization of energy intake rate: the contingenty model

Table 3. Effects of factors on fit of data to optimal diet theory

Factor	Quantitative tests of theory: Échelle: 1-6* mean (SE)	Quantitative tests of theory: Statistical test	Qualitative tests of theory: Échelle: 1-3* mean (SE)	Qualitative tests of theory: Statistical test
Site of study				
Laboratory	4.00 (0.21)	U=159	2.31 (0.11)	U=1039.5
Field	3.89 (0.43)	P=0.84	2.52 (0.11)	P=0.14
Experiment?				
Yes	3.94 (0.21)	U=151	2.31 (0.10)	U=894.5
No	3.94 (0.45)	P=0.95	2.60 (0.12)	P=0.06
Forager				
Invertebrate	3.67 (0.33)	τ=0.086	2.38 (0.13)	τ=0.060
Ectothermic vertebrate	3.63 (0.63)	NS	2.37 (0.16)	NS
Endothermic vertebrate	4.08 (0.28)		2.47 (0.12)	
Prey				
Immobile	4.22 (0.33)	τ=−0.212	2.61 (0.10)	τ=−0.229
Essentially immobile	4.25 (0.48)	P=0.08	2.40 (0.19)	P<0.005
Slightly mobile	4.00 (0.47)		2.44 (0.20)	
Mobile	2.25 (0.48)		2.04 (0.17)	

*Higher scores indicate higher support to optimal diet theory.

Sih et Christensen 2001, Anim. Behav. 61: 379-390

Maximization of energy intake rate: the contingenty model

- Northwester crows feeding on littleneck clams
- Must find, then open the clams by dropping them on flat rock

(*Corvus caurinus*)

(*Venerupis japonica*)

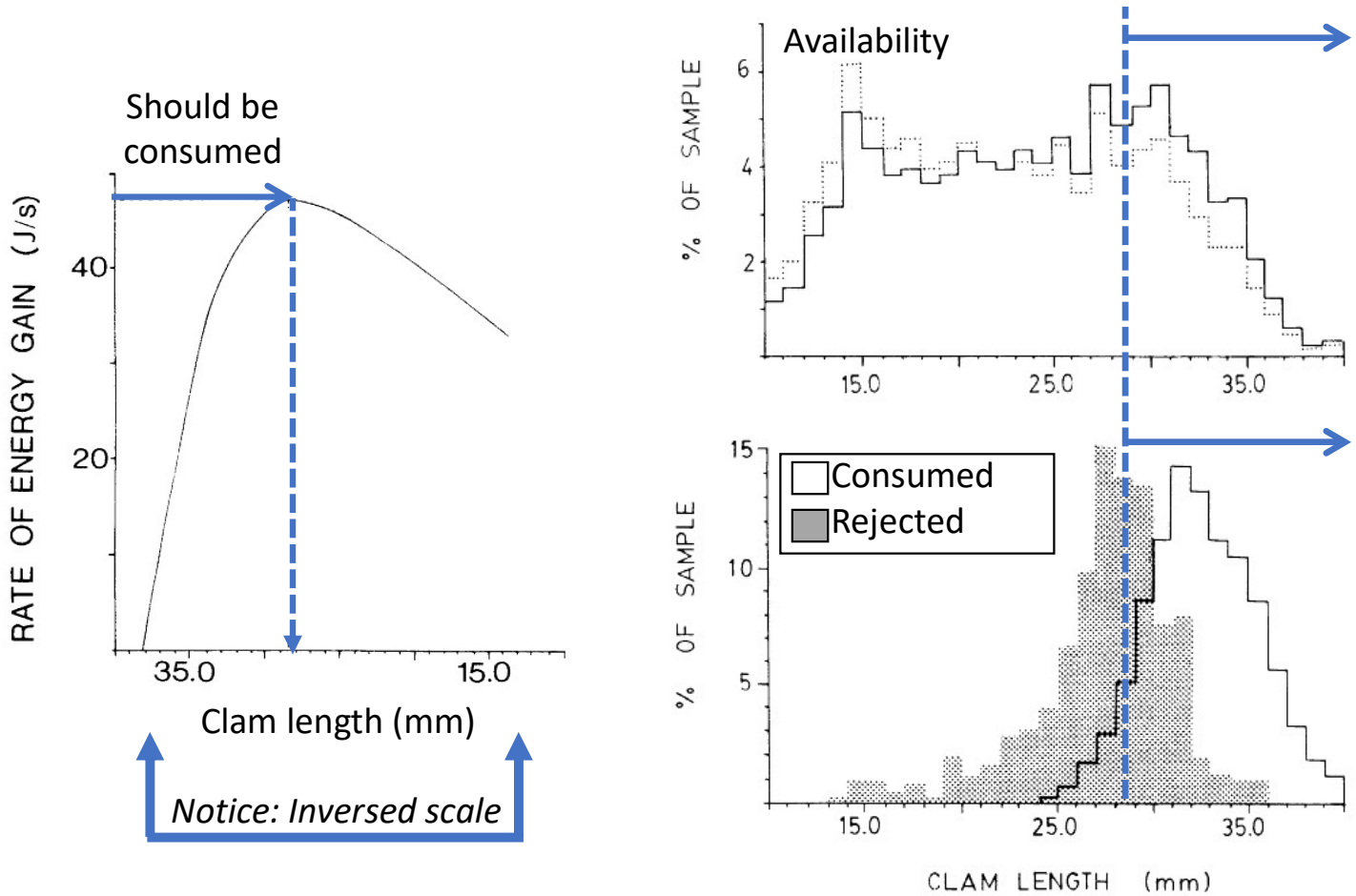
Richardson and Verbeek (1986, Ecology 67: 1219-26)

Maximization of energy intake rate: the contingenty model

- 34.6 sec to find a clam
- 4.2 sec first drop flight
- 5.5 sec handling between drops
- Flight costs > 4x higher than search and dig costs

Richardson and Verbeek (1986, Ecology 67: 1219-26)

Maximization of energy intake rate: the contingenty model



Maximization of energy intake rate: the contingenty model

Some assumptions of the contingency model:

- Omniscience
- Successive encounters with resources are independent events (e.g., not distributed in patches)
- No predation

Maximization of energy intake rate: the contingenty model

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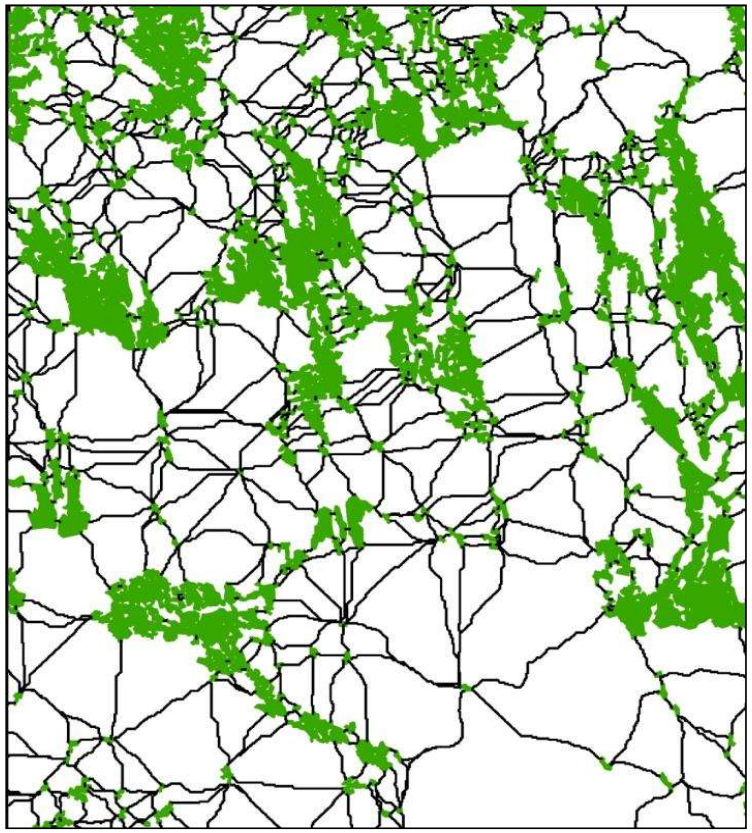
What if prey forage in a mosaic of food patches in which > 1 resource type is available?



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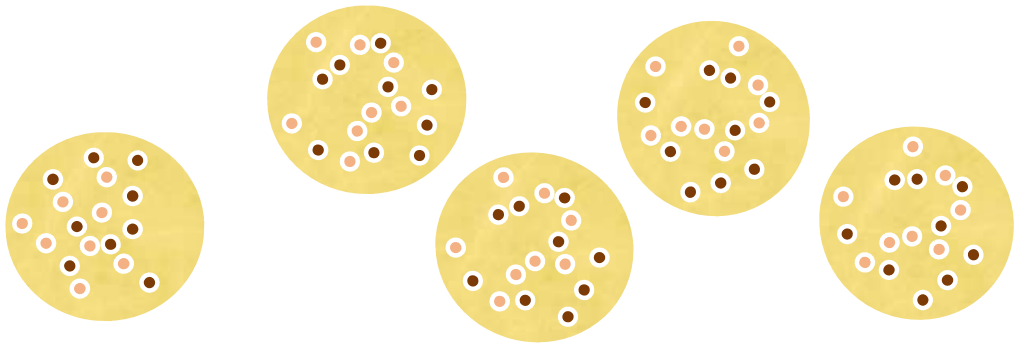

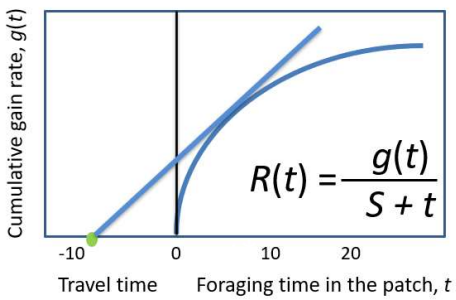

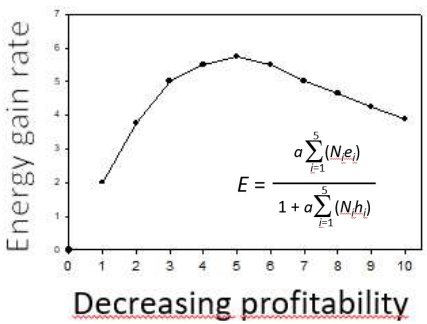

$g(t^*)$

$g(t^*)$ depends on food choice

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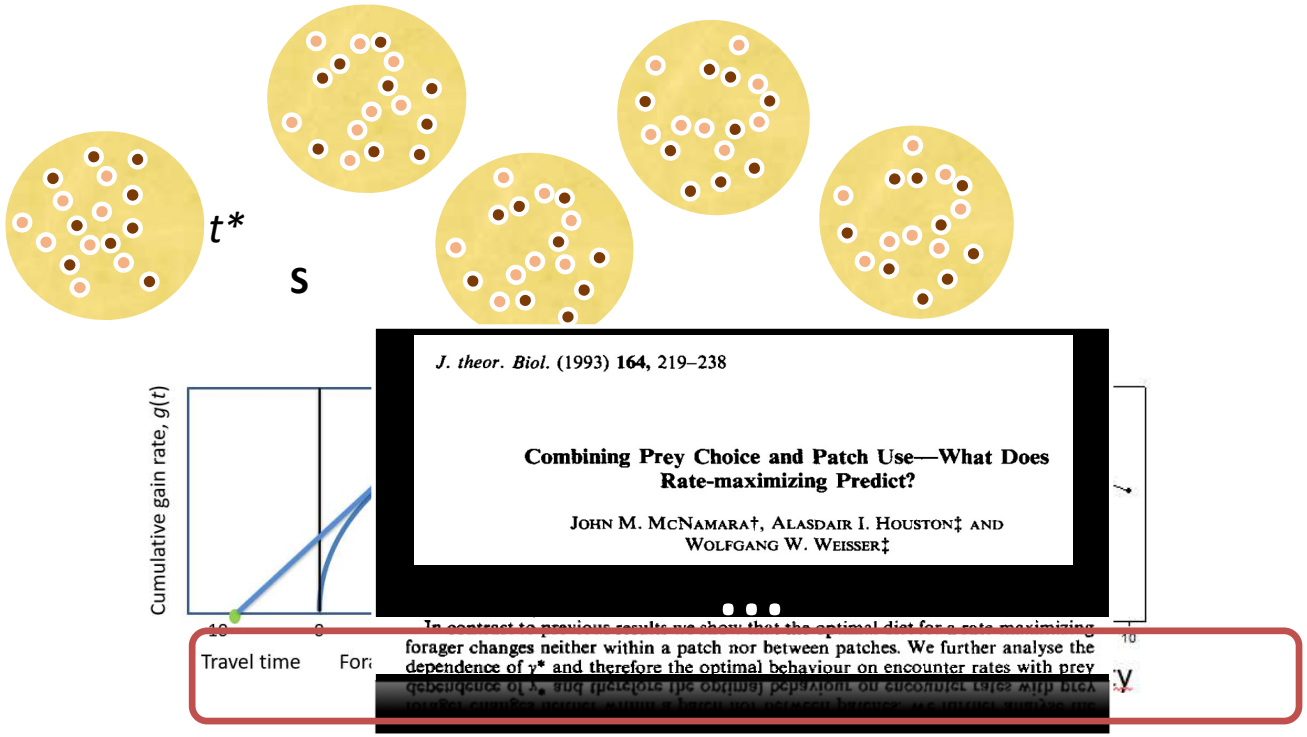

$$g(t^*) = \sum_{i=1}^{t^*} E_t^*$$

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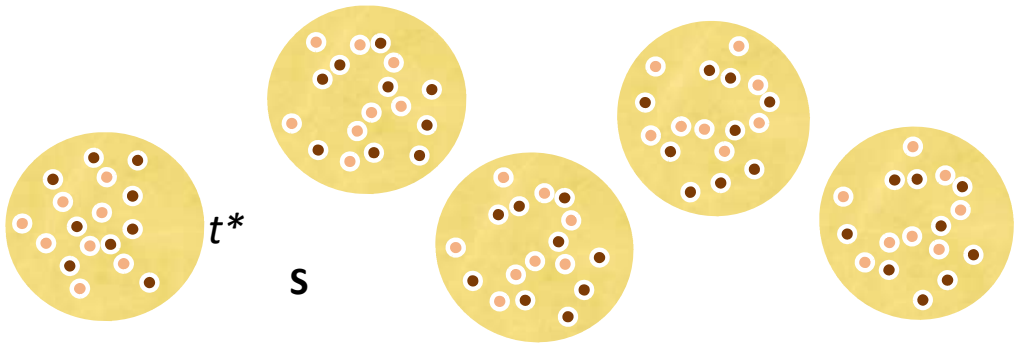
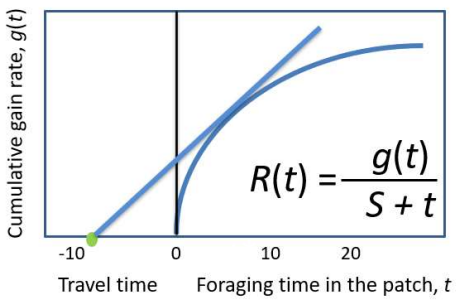
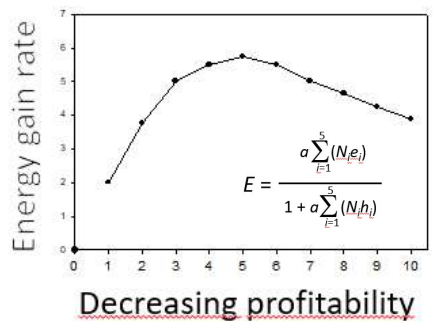






$$R(t^*) = \frac{g(t^*)}{S + t^*}$$

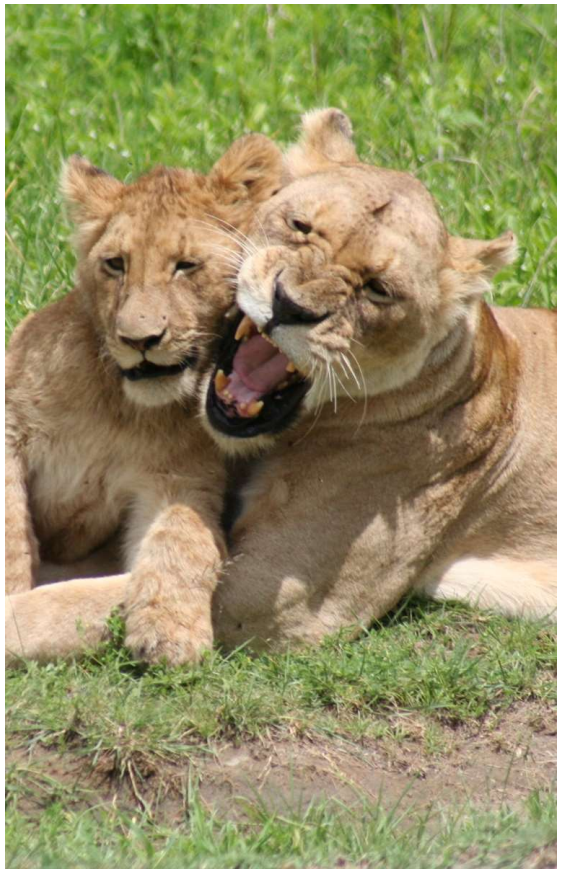
$$g(t^*) = \sum_{i=1}^{t^*} E_t^*$$

$$R(t^*) = \frac{\sum_{i=1}^{t^*} E_t^*}{S + t^*}$$

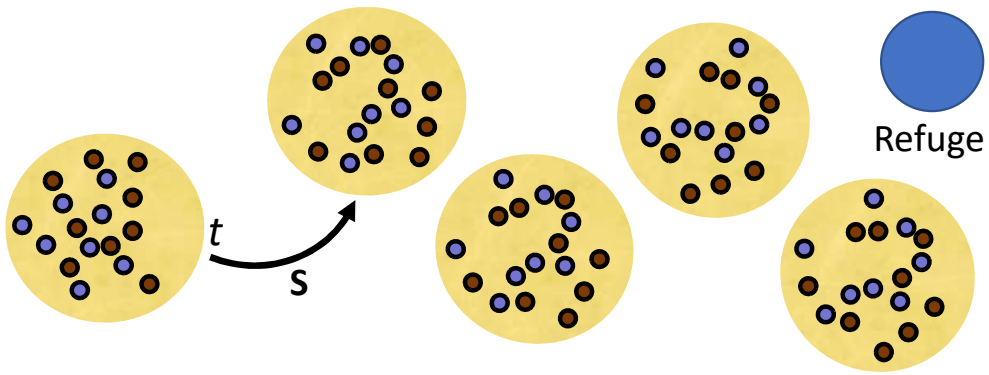
Maximization of energy intake rate: the contingenty model

Some assumptions of the contingency model:

- Omniscience
- Successive encounters with resource are independent events (e.g., not distributed in patches)
- No predation



What if a predator enters the system, and prey have access to refuges?

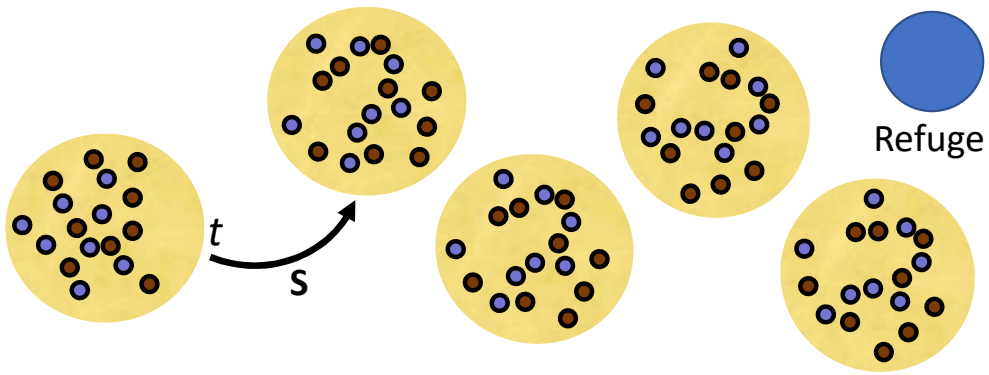


$$R(t) = \frac{T_s \boxed{aN} g(t)}{\boxed{T_s + T_h + T_r} \rightarrow T_f}$$

$$R(t) = \frac{T_s\, aN\, g(t)}{T_s + aNT_s t + T_r} = \frac{aN\, g(t)}{1 + aNt + T_r/T_s}$$

T_s: total time spent searching (min)
T_h: total time foraging in paches (min)
T_r: total time spent in refuges (min)
$\boxed{aN} = \lambda$: patch encounter rate (patches/min)

What if a predator enters the system, and prey have access to refuges?



$$R(t) = \frac{aN\,g(t)}{1 + aNt + T_r/T_s}$$

$$\mu = \frac{T_s\mu_s + T_h\mu_h + T_r\mu_r}{T_s + T_h + T_r}$$

We can then find: $E^*_{realized} = R(t^*)\mu$ i.e. $E^*_{realized}$ is the currency to maximize.

T_s: total time spent searching (min)
T_h: total time foraging in patches (min)
T_r: total time spent in refuges (min)
$aN = \lambda$: patch encounter rate (patches/min)

μ: Probability of surviving to realize the gain
μ_s: Pr. surviving when → searching food
μ_h: … when → feeding in a patch
μ_r: … when → staying in a refuge

The interacting phenotype approach

FM0

Initially evolutionary biology for animal breeders (mostly)

Diapositive 46

FM0 Je crois que cette section pourrait être un peu mieux centrée sur des exemples concrets appliqués aux interactions prédateur-proie et moins théorique.

Par exemple, on pourrait utiliser un exemple concret pour la section sur les figures et les différentes droites
Fraser Franco, Maxime; 2023-04-25T13:54:43.612

FM0 0 Je suggère aussi des références + fondamentales sur les modèles utilisés:

Modèle hiérarchiques doubles
- Cleasby et al. 2015
- Westneat et al. 2014
- Lee and Nedler 2006

Modèles multivariés
- Dingemanse and Dochtermann 2013
- Mitchell and Houslay 2020
Fraser Franco, Maxime; 2023-04-25T13:55:20.174

2) The interacting phenotype approach

- Comes from quantitative genetics
  - Aims to predict micro-evolutionary changes in traits
  - Considers two components:
    - Phenotypic/genetic variation
    - Selection
- Recently, expanded to analyse phenotypic variation over ecological timescales
    - Decomposes phenotypic variation into variation coming from genetic differences, developmental plasticity, and flexibility

Falconer 1981, Lynch and Walsh 1998, Réale et al. 2007, Dingemanse et al. 2010

The basics

- Analysing the average behaviour of a population (mean behaviour, developmental plasticity, flexibility). For example predator activity:

$$p = \mu + \varphi_{dev} Env_{dev} + \varphi_{flex} Env_i + \varepsilon$$
$$\varepsilon \sim N(0, \sigma_\varepsilon^2)$$

- Modelling individual variation within this population (we add individual differences in average behaviour, plasticity, and flexibility

$$p = \mu + a_i + \varphi_{dev} Env_{dev} + \varphi_{dev,i} Env_{dev} + \varphi_{flex} Env_{flex} + \varphi_{flex,i} Env_{flex} + \varepsilon$$
$$\varepsilon \sim N(0, \sigma_\varepsilon^2)$$

φ_{dev} and φ_{flex} = the slope of a linear regression of behaviour against the environmental values (i.e. a reaction norm).

ε = A stochastic deviation from the predicted behavioural value.

Robertson 1966, Price 1970, Falconer 1981, Lande and Arnold 1983, Lynch and Walsh 1998

The extensions

- Recently, expanded to analyse phenotypic variation over ecological timescales

$$\sigma_p^2 = \sigma_A^2 + \sigma_{NA}^2 + \sigma_{ind}^2 + \sigma_{env}^2 \psi^2 + \sigma_{Stoc}^2$$

  - Old work: individuals can switch their response based on interaction or habitat structure (plasticity, generates within individual differences)
  - Recent work: individuals differ in their average behaviour (personality, among individual differences)
  - Even more recent work: individuals differ in their plasticity

Greef and Whiting 2000, Réale et al. 2007, Dingemanse et al. 2010

The basics

- Estimating the selection differential (change in $\bar{p}$ within generations)

$$S = \beta\ \sigma_p^2$$

- Estimating the evolutionary response (change in $\bar{p}$ between generations)

$$\Delta p = S\ h_p^2$$

β = the slope of a linear regression of fitness against the phenotypic values.

σ_p^2 = the phenotypic variance or the genetic additive variance of the trait.

h_p^2 = the heritability of the trait (σ_A^2 / σ_p^2).

Robertson 1966, Price 1970, Falconer 1981, Lande and Arnold 1983, Lynch and Walsh 1998

proof

- When we integrate individual variation in plasticity

$$\sigma_p^2 = \sigma_A^2 + \sigma_{NA}^2 + \sigma_{ind}^2 + \sigma_{env}^2 \sigma_{\psi}^2 \sigma_{env}^2 \overline{\psi}^2 + \sigma_{Stoc}^2$$

- Proof:

$$\sigma_p^2 = \sigma_{a+\beta x}^2 + \sigma_{Stoc}^2 = \sigma_{\beta x}^2 + \sigma_{Stoc}^2$$

$$\sigma_p^2 = \sigma_{\overline{\beta} X + \beta_{ind} X}^2 + \sigma_{Stoc}^2 = \sigma_{\overline{\beta} X + \beta_{ind} X}^2 + \sigma_{Stoc}^2$$

$$\sigma_p^2 = \beta^2 \sigma_x^2 + \sigma_x^2 \sigma_{\beta_{ind}}^2 + \sigma_x^2 \overline{\beta_{ind}}^2 + \sigma_{\beta_{ind}}^2 \bar{x}^2$$

- If x and bind are centered on 0:

$$\sigma_p^2 = \beta^2 \sigma_x^2 + \sigma_x^2 \sigma_{\beta_{ind}}^2$$

Quantifying behavioural variation & selection

FM0

- Using hierarchical models (estimate individual behavioural reaction norm)

$$p_{ij} \sim a + b_1 x_1 + a_i + b_{1i} x_1 + e_{ij}$$

$$\begin{matrix} a_i \\ b_i \end{matrix} \sim N\left(\begin{matrix} 0 \\ 0 \end{matrix}, \begin{matrix} \sigma^2_{Intercept} & \sigma_{Int,slope} \\ \sigma_{Int,slope} & \sigma^2_{slope} \end{matrix}\right)$$

$$e_{ij} \sim N(0, \sigma^2_r)$$

Lee and Nedler 2006, Dingemanse & Dochtermann 2012, Westneat et al. 2014, Cleasby et al. 2015

FM1

Diapositive 52

FM0 Ici ça serait plutôt double-hierarchical (generalized) linear models. Mixed et hierarchical veulent dire deux choses relativement semblables.
Fraser Franco, Maxime; 2023-04-25T13:43:21.804

FM1 On n'a pas fait de modèles doubles dans mon article.
Fraser Franco, Maxime; 2023-04-25T13:44:52.725

Quantifying behavioural variation & selection

FM0

- Using hierarchical models (estimate individual behavioural profile, reaction norm, and intra-individual variability)

Mean model

$$p_{ij} \sim a + b_1 x_1 + a_i + b_{1i} x_1 + e_{ij}$$

$$\begin{matrix} a_i \\ b_i \end{matrix} \sim N\left(\begin{matrix} 0 \\ 0 \end{matrix}, \begin{matrix} \sigma^2_{Intercept} & \sigma_{Int,slope} \\ \sigma_{Int,slope} & \sigma^2_{slope} \end{matrix} \right)$$

Dispersion model

$$e_{ij} \sim N(0, \sigma^2_r)$$

$$\sigma = a_r + a_{ri}$$

Lee and Nedler 2006, Dingemanse & Dochtermann 2012, Westneat et al. 2014, Cleasby et al. 2015

FM1

Diapositive 53

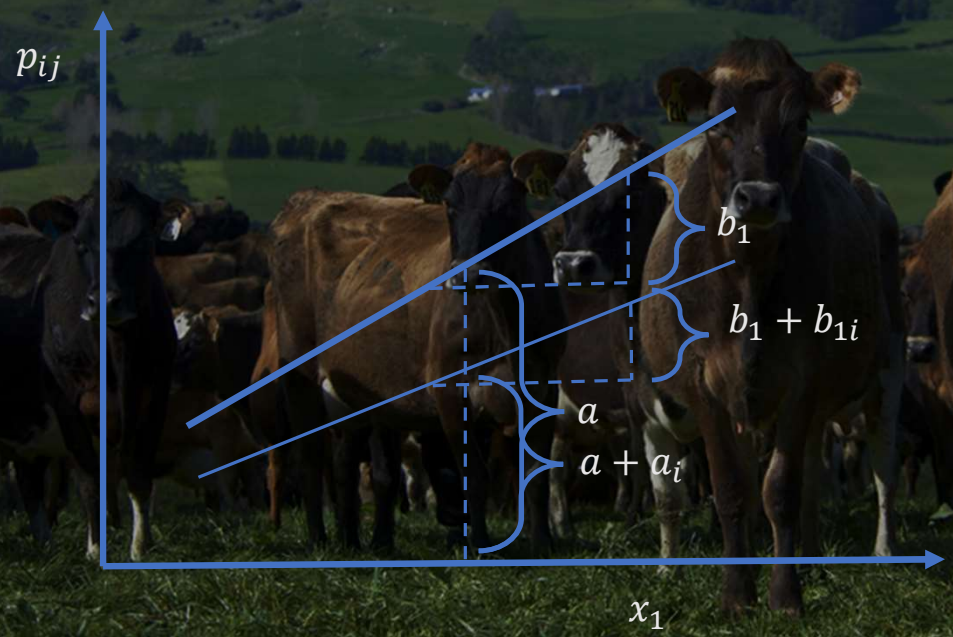
FM0 Ici ça serait plutôt double-hierarchical (generalized) linear models. Mixed et hierarchical veulent dire deux choses relativement semblables.
Fraser Franco, Maxime; 2023-04-25T13:43:21.804

FM1 On n'a pas fait de modèles doubles dans mon article.
Fraser Franco, Maxime; 2023-04-25T13:44:52.725

Quantifying behavioural variation & selection

- What does this mean?

$$\widehat{p_{ij}} \sim a + b_1 x_1 + a_i + b_{1i} x_1$$



Lee and Nedler 2006, Dingemanse & Dochtermann 2012, Westneat et al. 2014, Cleasby et al. 2015

Quantifying behavioural variation & selection

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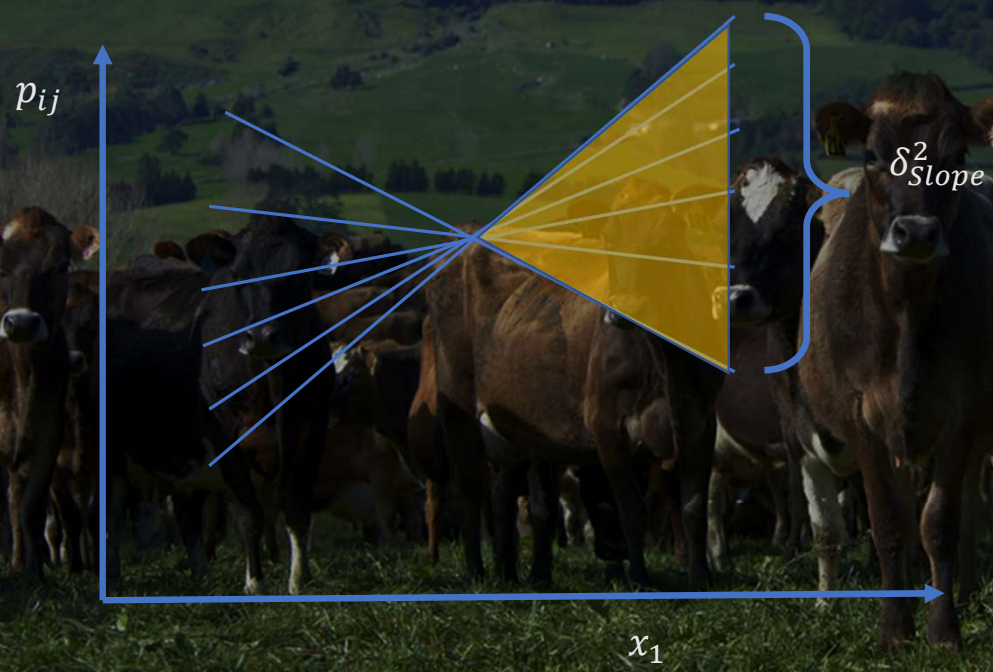

Lee and Nedler 2006, Dingemanse & Dochtermann 2012, Westneat et al. 2014, Cleasby et al. 2015

Quantifying behavioural variation & selection

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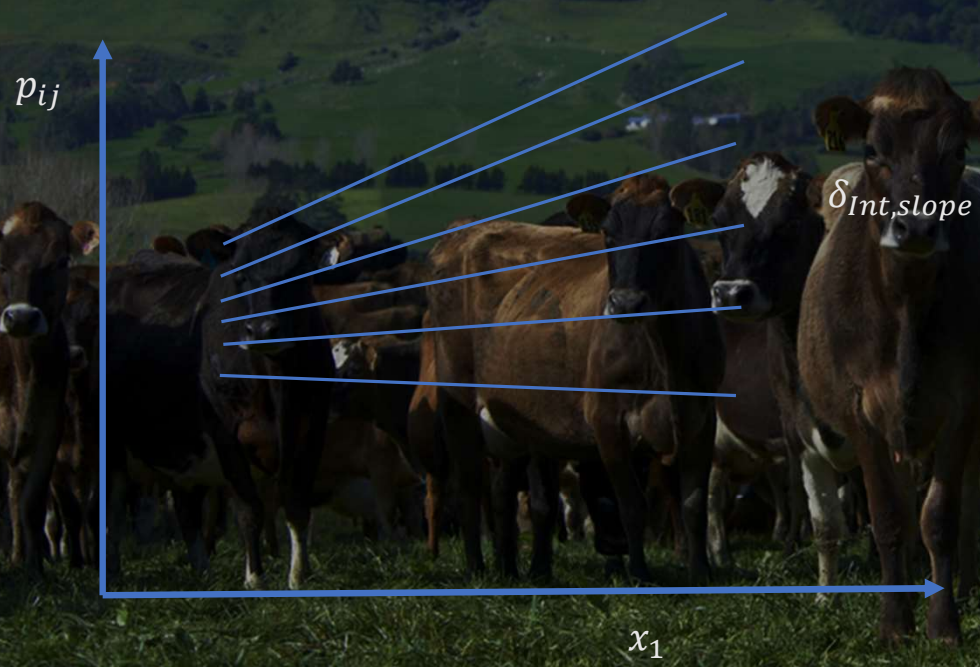

Lee and Nedler 2006, Dingemanse & Dochtermann 2012, Westneat et al. 2014, Cleasby et al. 2015

Quantifying behavioural variation & selection

- What does this mean?

$$\sigma_r^2 = a_r + a_{ri}$$

Lee and Nedler 2006, Dingemanse & Dochtermann 2012, Westneat et al. 2014, Cleasby et al. 2015

Going multivariate

$$\begin{matrix} p_{ij} \\ q_{ij} \end{matrix} \sim \begin{matrix} a_p \\ q_p \end{matrix} + \begin{matrix} b_{1p} \\ b_{1q} \end{matrix} x_1 + \begin{matrix} a_{pi} \\ a_{qi} \end{matrix} + \begin{matrix} b_{1pi} \\ b_{1qi} \end{matrix} x_1 + \begin{matrix} e_{pij} \\ e_{qij} \end{matrix}$$

$$\begin{matrix} a_{pi} \\ b_{1pi} \\ a_{qi} \\ b_{1qi} \end{matrix} \sim N \left(\begin{matrix} 0 \\ 0 \\ 0 \\ 0 \end{matrix}, \begin{matrix} \sigma^2_{a_{pi}} & \sigma_{a_{pi}b_{1pi}} & \dots & \dots \\ \sigma_{a_{pi}b_{1pi}} & \sigma^2_{b_{1pi}} & \dots & \dots \\ \dots & \dots & \sigma^2_{a_{qi}} & \sigma_{a_{pi}b_{1pi}} \\ \dots & \dots & \sigma_{a_{pi}b_{1pi}} & \sigma^2_{b_{1qi}} \end{matrix} \right)$$

$$\begin{matrix} e_{pi} \\ e_{qij} \end{matrix} \sim N \left(\begin{matrix} 0 \\ 0 \end{matrix}, \begin{matrix} \sigma^2_{pr} & \sigma_{pr,qr} \\ \sigma_{pr,qr} & \sigma^2_{qr} \end{matrix} \right)$$

$$\begin{matrix} \sigma^2_{pr} \\ \sigma^2_{qr} \end{matrix} = \begin{matrix} a_{pr} \\ a_{qr} \end{matrix} + \begin{matrix} a_{pri} \\ a_{qri} \end{matrix}$$

Dingemanse and Dochtermann 2013, Mitchell and Houslay 2020

Estimating linear selection

$$\begin{matrix} p_{ij} \\ w_{ij} \end{matrix} \sim \begin{matrix} a_p \\ a_w \end{matrix} + \begin{matrix} b_{1p} \\ b_{1w} \end{matrix} x_1 + \begin{matrix} a_{pi} \\ a_{wi} \end{matrix} + \begin{matrix} b_{1pi} \\ b_{1wi} \end{matrix} x_1 + \begin{matrix} e_{pij} \\ e_{wi} \end{matrix}$$

$$\begin{matrix} a_{pi} \\ b_{1pi} \\ a_{wi} \\ b_{1wi} \end{matrix} \sim N \left(\begin{matrix} 0 \\ 0 \\ 0 \\ 0 \end{matrix}, \begin{matrix} \sigma^2_{a_{pi}} & \dots & \dots & \dots \\ \sigma_{a_{pi} b_{1pi}} & \sigma^2_{b_{1pi}} & \dots & \dots \\ \sigma_{a_{pi}, a_{wi}} & \sigma_{b_{1p}\, a_{wi}} & \sigma^2_{a_{wi}} & \dots \\ \sigma_{a_{pi} b_{1wi}} & \sigma_{b_{1pi} b_{1w}} & \sigma_{a_{wi} b_{1wi}} & \sigma^2_{b_{1wi}} \end{matrix} \right)$$

$$\begin{matrix} e_{pij} \\ e_{wij} \end{matrix} \sim N \left(\begin{matrix} 0 \\ 0 \end{matrix}, \begin{matrix} \sigma^2_{pr} \\ \sigma^2_{wr} \end{matrix} \right)$$

Dingemanse and Dochtermann 2013, Mitchell and Houslay 2020

Estimating linear selection

$$\begin{matrix} p_{ij} \\ w_{ij} \end{matrix} \sim \begin{matrix} a_p \\ a_w \end{matrix} + \begin{matrix} b_{1p} \\ b_{1w} \end{matrix} x_1 + \begin{matrix} a_{pi} \\ a_{wi} \end{matrix} + \begin{matrix} b_{1pi} \\ b_{1wi} \end{matrix} x_1 + \begin{matrix} e_{pij} \\ e_{wij} \end{matrix}$$

$$\begin{matrix} a_{pi} \\ b_{1pi} \\ a_{wi} \\ b_{1wi} \end{matrix} \sim N \left(\begin{matrix} 0 \\ 0 \\ 0 \\ 0 \end{matrix}, \begin{matrix} \sigma^2_{a_{pi}} & \dots & \dots & \dots \\ \sigma_{a_{pi}b_{1pi}} & \sigma^2_{b_{1pi}} & \dots & \dots \\ \sigma_{a_{pi},a_{wi}} & \sigma_{b_{1pi}a_{wi}} & \sigma^2_{a_{wi}} & \dots \\ \sigma_{a_{pi}b_{1wi}} & \sigma_{b_{1pi}b_{1w}} & \sigma_{a_{wi}b_{1wi}} & \sigma^2_{b_{1wi}} \end{matrix} \right)$$

$$\begin{matrix} e_{pij} \\ e_{wij} \end{matrix} \sim N \left(\begin{matrix} 0 \\ 0 \end{matrix}, \begin{matrix} \sigma^2_{pr} & \sigma_{pr,qr} \\ \sigma_{pr,qr} & \sigma^2_{qr} \end{matrix} \right)$$

$$\begin{matrix} \sigma^2_{pr} \\ \sigma^2_{qr} \end{matrix} = \begin{matrix} a_{pr} \\ a_{qr} \end{matrix} + \begin{matrix} a_{pri} \\ a_{qri} \end{matrix}$$

Dingemanse and Dochtermann 2013, Mitchell and Houslay 2020

Integrating the two approaches…

And collaborating to analyse data from TrophEE

Where to go from here

- We need more empirical work
- Models can become more useful to empiricists:
  - Consider different fitness architecture of predator/prey traits (costs and benefits).
  - Introduce spatial / temporal heterogeneity and food web structure
  - Integrate multiple predator / prey traits interacting to affect capture
- We need to understand the consequences of individual variation
  - What are the consequences of individual variation for predator-prey coevolution?
  - What is the impact of cognitive mechanisms on coevolution?

Abrams 2010, McNamara 2022,

Key areas for collaborations

- Using the TrophEE game to integrate optimality and interacting phenotype approaches
  - Are we optimal when we play? Do we adjust our behaviour to changes in handling time or refuge safety?
  - Is optimal foraging theory a useful framework in such complex systems?
  - What is the selection imposed by prey on predator behaviour (and vice versa)?
  - What are the consequences of individual variation in a species for the variation in the other species?
  - Can we improve our tactics from social information, or simply as we gain experience playing the game?

- Littérature d'écologie comportementale :
- • Context-dependent trait covariances: how plasticity shapes behavioral syndromes
- • Biologging reveals individual variation in behavioural predictability in the wild
- • A guide for studying among-individual behavioral variation from movement data in the wild
- • Studying predator foraging mode and hunting success at the individual level with an online videogame
- • Quantifying individual variation in behaviour: mixed-effect modelling approaches
- Littérature de génétique quantitative :
- • Indirect genetics effects and evolutionary constraint: an analysis of social dominance in red deer, Cervus elaphus
- • Genetic variance for behavioural ‘predictability’ of stress response
- • Indirect genetic effects and the evolution of aggression in a vertebrate system